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USE OF ROOTED CUTTINGS IN REFORESTATION

A REVIEW OF OPPORTUNITIES PROBLEMS AND ACTIVITIES

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ABSTRACT

Physiology of maturation in woody plants is discussed in relation to the desirability of retaining juvenility, which generally confers higher rooting potential and growth rates on cuttings. Reforestation with rooted cuttings allows retention of both additive and non-additive gene effects of selected trees, whereas the additive effect is retained only in sexual reproduction. For many species, this advantage must be set against a possible decrease in growth rate, because of tree maturation and a poor growth form; also, production costs for rooted cuttings are generally higher than for seedlings. A reforestation program with rooted cuttings could take at least 10 years from initiation to large-scale field use.

Reforestation with rooted cuttings has been common in Japan for centuries and has comprised 120 million Cryptomeria plants in 1966/67. A million spruce rooted-cuttings are produced annually in West Germany from selected clones, and a similar program has been started in Finland. Relevant research has been undertaken in other countries, notably New Zealand and Australia.

Reforestation in British Columbia with rooted cuttings is discussed for Douglas-fir, western hemlock, white spruce, lodgepole pine, Sitka spruce and yellow cedar. Possible advantages are that rooted cuttings can be used when availability and quality of seed becomes critical (yellow cedar), and results from tree improvement programs can be utilized more quickly in cases where seed production in seed orchards is slow (Douglas-fir, western hemlock, Sitka spruce). The long-term incentive depends on the importance of non-additive genetic inheritance and only scant information on this is available for two species (Douglas-fir and western hemlock). A major disadvantage could result from a decrease in growth potential with tree maturation, but this, together with possible means of overcoming it, have not been studied for the British Columbia species.

RÉSUMÉ

Le présent travail étudie la physiologie de la maturation relativement au caractère désirable de conservation de la jeunesse, qui confère généralement aux boutures un meilleur potentiel e'enracinement et de taux de croissance. La restauration forestière au moyen de boutures permet de retenir à la fois les effets génétiques additifs et non-additifs des arbres choisis, tandis que l'effet additif est retenu seulement par la reproduction sexuelle. Chez plusieurs espèces, cet avantage doit s'opposer à une diminution possible du taux de croissance, due à la maturation des arbres et à une forme de croissance médiocre; de plus, les coûts de production des boutures enracinées sont habituellement plus élevés que pour les semis. Un programme de restauration forestière au moyen de boutures pourrait e'échelonner sur une période de 10 ans, à partir des opérations premières jusqu'a l'utilisation du terrain sur une grande échelle.

Le Japon a utilisé communément cette méthode durant plusieurs siècles et on comptait 120 millions de semis de Cryptomeria en 1966/67. l'Allemagne de l'Ouest produit annuellement un million de boutures enracinées provenant de clones choisis et un programme semblable a été inauguré en Finlande. D'autres pays, notamment la Nouvelle-Zélande et l'Australie ont entrepris des recherches dans le même sens. En Colombie Brittannique, on étudie à ce propos le Douglas taxifolié, la Pruche occidentale, l'Epinette blanche, le Pin tordu, l'Epinette de Sitka et le Cyprès jaune, pour la restauration forestière. On pourrait utiliser des boutures lorsque l'approvisionnement et la qualité des graines deviennent critiques (Cyprès jaune), puis les produits des programmes d'amélioration des arbres sont disponibles plus rapidement dans les cas où la production des vergers à graines est lente (Douglas taxifolié, Pruche occidentale, Epinette de Sitka). L'incitation à long terme dépend de l'importance de l'amélioration génétique non-additive, mais on possède des renseignements - d'ailleurs insuffisants - sur seulement deux espèces: le Douglas taxifolié et la Pruche occidentale. Il pourrait se produire un inconvénient sérieux dû à la diminution du potentiel de croissance associée à la maturation des arbres, mais eu égard aux espèces de la Colombie-Britannique, on n'a pas encore analysé cette éventualité.

INTRODUCTION

Interest in the use of rooted cuttings for reforestation has recently increased in many parts of the world. This use began about the year 1400 in Japan, with Cryptomeria japonica. Reforestation with cuttings of various poplars has been done extensively in many countries for a long time; however, this review will be limited to conifers. At present, extensive forest establishment by this means is confined to Japan, with small-scale use also in West Germany. Indications are, however, that the operational large-scale use of cuttings in reforestation will soon increase considerably for many conifers which lend themselves readily to cutting propagation. The review is not concerned with vegetative propagation where this is only an intermediate step, such as in seed orchard and clone bank establishment, and is not the final step in the production of reforestation stock.

This report considers, firstly, opportunities and problems associated with cutting use in reforestation; secondly, activities in various countries, and thirdly, it evaluates the British Columbia situation. The final section gives conclusions and recommendations for research. This review and problem analysis is intended primarily for researchers, research managers and foresters concerned with reforestation and tree improvement in British Columbia, but it is also intended to be of use to others with similar interests.

I OPPORTUNITIES AND PROBLEMS

Significance of maturation and ageing to rooting and growth rate of tree cuttings.

In the propagation of forest trees by means of rooted cuttings, the age and size of the donor tree, or ortet, and the position from which the cutting is excised are important. The reasons for this will become clear if the changes known to occur with age are examined.

In many woody plants, a juvenile and an adult state can be distinguished by such characters as leaf shape and phyllotaxy, ease of rooting of cuttings, thorniness, growth habit, leaf retention in deciduous species, and flowering (Schaffalitzky de Muckadell 1954; Wareing 1959; Doorenbos 1960; Brink 1962). This change from juvenile to adult, which may be relatively abrupt, is called "phase change" (Brink 1962). In considering trees, Wareing (1959) thought it desirable to distinguish between this juvenile to adult change which he called "maturation", and loss of vigor because of increasing size and complexity which he called "ageing". He suggested that, while changes resulting from ageing can be reversed by means of vegetative propagation, those resulting from maturation usually can not.

The difference between phase change and ageing is not strongly emphasized by Doorenbos (1960), who found that reversion from the adult to the juvenile state in ivy (Hedera helix) can be induced by grafting together material from the two phases. He considered that the general effects of ageing can be, at least partly, explained by the effect of nutrition operating through the shoot apex.

Changes in the various criteria, such as ease of rooting, ability to flower, growth rate, etc., used to distinguish between juvenile and adult phases, do not occur simultaneously. This resulted in the suggestion that there are various relatively independent overlapping phases instead of one juvenile phase (Borchert 1967). The importance of increase in tree size and complexity was stressed in explaining many of the apparently unrelated morphological and physiological changes that others have sought to attribute to a single phase change (Borchert 1976).

In contemplating the possibility of controlling phase change and inducing phase reversal, with its associated advantages, the question of genetic control arises. How can two different, relatively stable phenotypes exist at different periods of development within a plant having a single genome? Wareing (1959) argued that since tissues can exist in juvenile or adult states, there must be transmission of a given state by cell lineage through a number of cell generations. This would be explained by postulating a self-duplicating cytoplasmic inheritance factor. Similarly, Brink (1962) considered that phase change indicated chromosomes must serve a genetic function, concerned with heredity, and a paragenetic function, concerned with development of the individual.

Libby (1974b) suggested that maturation is caused by the accumulation of relatively irreversible genetic state changes in the plant's DNA. Usually the DNA only reverts to a cleared "ground state" at, or about, meiosis. Certainly juvenility is always restored during sexual reproduction (Brink 1962). In Citrus, however, embryos may be formed from nucellar (i.e., adult) tissue without meiosis (Robbins

1957; Borchert 1967), so that the reversal to juvenile condition in Citrus, at least, is not dependent on meiosis.

Reversal from adult to juvenile phase can apparently occur under certain conditions, for example, in ivy and juniper (Doorenbos 1960; Brink 1962) and in Acacia melanoxylon (Borchert 1967), and it would be convenient if this reversal could be induced in cuttings removed from selected adult trees. The advantages of easier rooting and juvenile growth rate would be obtained. In fact, there is no evidence that phase reversal occurs in commercially important forest trees, but retardation of phase change from juvenile to adult state may be possible. In older trees, a basal, cone shaped, juvenile zone generally persists (Schaffalitzky de Muckadell 1954), while the peripheral branches are in a mature condition. For example, shoots at the base of old beech (Fagus sylvatica) trees retain their foliage (a juvenile trait) during much of the winter, and flowers and cones are normally not borne on the basal part of a tree. The existence of juvenile and mature phases in a single tree implies that cuttings removed from the basal juvenile zone may root more readily and show other juvenile characteristics (Doorenbos 1960; Hartmann and Kester 1975). This is supported by several reports which indicate that cutting back or grazing prolong the juvenile phase of growth (Schaffalitzky de Muckadell 1954; Doorenbos 1960). Evidently wild olive trees may be kept dwarfed and juvenile for more than 50 years, owing to continuous browsing by cattle (Natividade 1957), and hedges often give better rooting cuttings than plants of the same age that are allowed to develop without shearing (Garner and Hatcher 1955; Matthews 1952). According to Carr and Pate (1967), grazing or pruning prolongs the juvenility of the plant by forcing growth of axillary buds which are physiologically younger than the peripheral buds.

In practical terms, it is generally recognized that cuttings will root progressively more easily the younger the tree from which they are removed (Garner 1944; Satoo et al. 1953; Thulin and Faulds 1968; Sax 1962; Hartmann and Kester 1975), and advantage is being taken of the ability to retain juvenility by "hedging" forest trees. Useful clones of some forest tree species can be hedged to provide a source of juvenile material for cuttings (Libby et al. 1972; Kleinschmit et al. 1973; Ross 1975a). Pinus radiata cuttings from hedges continued to root with similar ease over a period of 6 years, and about as easily as cuttings from 4-year-old seedlings. In a comparison between cuttings from hedged and non-hedged trees of radiata pine, those from the hedged trees rooted best, and it was considered that hedging arrests the decline in rooting ability in this species (Libby et al. 1972). More recently, the value of hedging in reducing loss of juvenile growth vigor has also been demonstrated (Libby and Hood 1976).

The decline in rootability and growth rate of cuttings with age of ortets has also been retarded by repeated propagation of cuttings taken from rooted cuttings of radiata pine (Fielding 1969) and Douglas-fir (Black 1973). However, this technique was ineffective with white pine where five repeated cuttings, at 4-year intervals over the period 1938 to 1954, resulted in decrease in rooting ability each time (Delisle 1954). The procedure is worth further study in these and other species. Borchert (1967) also cites a technique for increasing rooting percentage of radiata pine short shoots. Evidently short shoots formed by restitution growth, after decapitating a branch tip, rooted four times as frequently as controls.

Grafts or rooted cuttings often show a slower growth rate the greater the age of the tree from which they were obtained. Evidence for this is cited by Schaffalitzky de Muckadell (1959, 1962), and is provided by his own work on beech (Fagus sylvatica) and ash (Fraxinus excelsior). This effect of increasing age reducing growth vigor was also demonstrated when cuttings of 10- and 30- to 35-year-old radiata pine were compared in a grafting experiment (Sweet 1964). Sweet (1973) and Sweet and Wells (1974) further showed that 2-year-old seedlings grew faster than 6-year or older rooted cuttings or grafts of the same species. They interpreted the data to mean that phase change from juvenile to adult state commenced early in ontogeny and proceeded gradually for some years. This noticeable effect of age in reducing growth vigor of vegetatively propagated radiata pine is supported by other work (Fielding 1969; Pawsey 1971; Shelbourne and Thulin 1974).

Studies on growth rates with other conifers are scarce and it is uncertain whether seed sources and clones were close enough genetically to make valid comparisons. Furthermore, the studies cover only a short time period. According to Toda and Isikawa (1971), Nagano (1962) found that cuttings of Pinus densiflora and Pinus thunbergii grew less than seedlings on the average for up to 5 years after planting. It was noted, however, that trees with the

greatest height were those grown from cuttings. Copes (1976) observed that seedlings and cuttings from juvenile Douglas-fir trees had similar growth rates of the leader for 4 to 6 years following field planting, but growth of cuttings from mature plus trees was considerably slower. Not all studies have indicated age-related decreases in growth rates. Observations with Scots pine and Siberian larch by Komissarov (1969) indicated that cuttings from 3-year-old seedlings were not inferior to seedlings in growth rate during the first 7 years. For Norway spruce, the growth rate of cuttings from young ortets has been as good as that of seedlings (Kleinschmit, pers. comm.). From this, it appears that trees of different species can be expected to vary in the age at which their growth potential is reduced and also in the degree of growth reduction, if any.

In using clonal material in reforestation, the problems of rootability and growth rate should be considered together. It is not sufficient to develop a technique, such as use of hormones in rooting, that will overcome one problem of maturation without solving the other. Also, it will be undesirable to root cuttings nearing the age at which rooting decreases if, thereby, we lose many years of a high juvenile growth potential. For example, in a species grown on a 60-year rotation, which shows loss of growth vigor associated with maturation changes after 20 years, it might be possible to root cuttings from 19-year-old material. This would be undesirable because growth would occur at the reduced "mature" rate throughout the life of the plantation. By contrast, a stand established from seedlings or cuttings from 2- or 3-year-old material would benefit from "high" juvenile growth rate for about one-third of the rotation.

Genetic gains

There is general agreement that vegetative propagation offers the possibility of rapid genetic improvement (Shelbourne and Thulin 1974; Libby et al. 1972; Thulin and Faulds 1968; Kleinschmit 1974; Rauter 1974; Roulund 1974; Ross 1975b). The reason for this is that the clones retain both the additive and non-additive gene effects of selected trees, whereas only the latter effects are retained in sexual reproduction. Therefore, if a superior genotype is identified, its superiority will be transmitted to all individuals produced by vegetative propagation, but it may take several generations of breeding and selection to produce a population of equal mean quality.

The non-additive components arise from dominant-recessive gene action and gene interactions (epistasis). With completely additive gene effects, the mean of the progeny will equal the mean of the parents for a given attribute, because the genes involved will have the same effects no matter how they are combined with other alleles. This does not happen with non-additive inheritance. Here, gene recombination may lead to segregation of undesirable recessives, or break up of favorable gene combinations. Consequently, the mean of a valuable attribute in the progenies regresses toward the mean of the population from which the parents were selected. The superiority of selected parents over the population mean for a given attribute is, therefore, only partly retained by the progenies resulting from sexual reproduction if non-additive inheritance is involved.

Genetic gains from various levels of selection have been calculated from experiments with Norway spruce in Germany (Kleinschmit 1974). A gain of about 20% can be expected by selecting the best provenances, a further 10% gain can be achieved at the level of half-sib families and at least another 10% by selection of individual clones.

A population based on selected clones will be genetically more uniform than one resulting from sexual reproduction (Roulund 1974). The desirability of this must be viewed in relation to the stand management applied. Although Toda (1974) agrees that clonal populations may be more uniform and of an initial better mean quality, he argues that thinning of stands derived from seedlings reverse this picture during the life of the stand. This is because thinning will take advantage of genetic diversity, present in stands of seedling origin, and leave only the better individuals for the final harvest. This upgrading of genetic quality may also take place through a natural selection without stand thinning. Toda also points out the biological risks in using clones and the greater long-term gain that can be achieved by tree breeding. These considerations have influenced the Japanese to rely more and more on seed than on cutting propagation for their tree improvement program; consequently, more of their scion orchards will be converted into seed orchards.

Since cuttings from most species root readily only when parent trees are young, and their growth potential may decrease with age of the parent, it is imperative that superior growth characteristics can

be recognized at an early age. This is still uncertain for important characteristics, such as volume production. Furthermore, superiority in one location is not sufficient assurance for performance on other sites, so estimates of genotype-site interaction should be provided by planting clonal propagules produced by cuttings on different sites (Burdon and Shelbourne 1974).

Root system quality

The root system of rooted cuttings is visually different from that of seedlings, usually having fewer and less branched main roots, with thicker and more brittle roots. Growth and survival in the field may therefore be affected. The quality of the root system in cuttings has been shown to decrease with age of the parent tree for Douglas-fir (Black 1973) and radiata pine (Thulin and Faulds 1968). Root systems have been improved by hedging of the parent trees (Libby et al. 1972) and by treatment of cuttings with auxin (Libby and Conkle 1966; Kiang et al. 1974). Time of cutting collection may also be important (Kiang et al. 1974).

Handling of cuttings with brittle roots could be difficult during lifting and transplanting; Thomas and Riker (1950) found that the horizontal and unilateral root system of white pine cuttings presented a problem. However, growth of cuttings in containers could overcome these difficulties (Hill and Libby 1969). Also, satisfactory root systems have been produced by root pruning (Thulin and Faulds 1968; Black 1973). It would seem, therefore, that proper propagation and nursery techniques can be found for production of satisfactory plants.

Growth form

Rooted cuttings of many conifers often retain a plagiotropic (branch-like) form for many years. Besides the species, form will depend on clone, ortet age, and crown position from which cuttings are taken (Black 1973). Obviously, plagiotropic growth would render the plants unsuitable for reforestation. An extreme case is reported for Araucaria excelsa R. Br., for which a side branch rooted more than 50 years ago still grew horizontally (Wareing 1959).

For cuttings from young trees of some conifers, such as Norway spruce (Kleinschmit 1974), plagiotropism is not pronounced, nor is it a problem with radiata pine (Fielding 1969). Douglas-fir cuttings from juvenile trees exhibit plagiotropic growth for some years. Ross (1975a) found that 60% of cuttings taken from sheared 1-year-old Douglas-fir seedlings grew at an angle of 60 to 90 degrees to the vertical during the year of rooting, but some had assumed an upright habit by the end of the first season. For cuttings from 4- to 8-year-old trees, more than 80% were plagiotropic 2 years after rooting but less than 15% after 7 years (Copes 1976). Black (1973) observed clonal differences; cuttings from some young clones grew normally after 3 years, while others required 6 to 10 years. Cuttings from old Douglas-fir trees can be expected to grow plagiotropically up to 10 years or more, and pruning and staking will not improve the form (Black 1973). About one-third of cuttings from mature western hemlock trees retained plagiotropic growth 6 years after rooting (Brix and Barker 1975).

Wood quality

Since rooted cuttings appear to retain the physiological maturity of the ortet, it is not surprising that they also maintain age-controlled wood properties (Nicholls and Brown 1971; Libby et al. 1972); this must be considered in evaluation of a program using cuttings. Further, the genetic uniformity in vegetative propagules will result in a more uniform wood product, which could be a technological advantage.

Pest implications

Use of cuttings in Japan was greatly increased about 1910 as a result of an outbreak of a needle blight disease, which was fatal to Cryptomeria seedlings but not to cutting-plants from older parents (Toda 1974). Similarly, a needle blight (Didymascella thujina) severely attacks Thuja plicata seedlings, but cuttings from the adult stage are highly resistant (Søegaard 1956).

Thus, cutting propagation offers a means of avoiding diseases and, presumably, insects which attack only juvenile trees. On the other hand, the genetic uniformity of clones may offer a biological risk. Toda (1974) cites a use in which a Cryptomeria clone had proved superior in growth rate over a period of 35 years; but, subsequently, when used extensively in reforestation, it was found to be very susceptible to stem canker and foliage mites. The biological risk can be reduced by including many clones in plantations or by mixing clones with seedlings of local origin. Conversely, trees proven resistant to particular diseases and insects can be quickly propagated vege-

tatively to produce resistant planting stock.

Cost

Thulin and Faulds (1968) estimated that the cost of producing plantable rooted cuttings of radiata pine is about three times that of seedling stock. At present, plantable Norway spruce cuttings are 2 to 3 times more expensive than seedlings in the Finnish program; with increased production and improvement in technique, the cost should decrease (Lepistö 1974). Kleinschmit et al. (1973) showed cost figures 30% higher for cuttings than for seedlings of Norway spruce. However, this is justified economically if the growth superiority of cuttings is 10% or more and this, the authors claim, should always be the case in a breeding program. Rauter (1974) felt that the genetic gain in using cuttings of black and white spruce would more than make up for the increased production cost.

Shortage of seed and problems in seed germination, as is presently experienced with yellow cedar in British Columbia (Edwards, pers. comm.), could cause a lower production cost of rooted cuttings than of seedlings. Furthermore, it should be considered that genetically improved material may warrant being planted at wider than normal spacing, thus reducing the reforestation cost per unit area (Kleinschmit 1974).

Kleinschmit (1974) compared the net profits from various tree improvement programs for Norway spruce. In spite of a higher plant cost, a cutting program was the most profitable, while a seed orchard program was least profitable for this species, mainly because of the long period (20 years) between grafting and seed production on an economic scale.

Time factors

The time required to research and develop a program depends on whether its purpose is rapid genetic improvement, as is generally the case, or a production of plants to supplement a scarce seed supply. Both objectives require the development of techniques for mass production of cutting material and for rooting of cuttings. The latter will include effect of parent age on rooting. Cultural techniques for nursery growth of rooted stock must be studied; one aspect of this will be growth performance in containers. Field performance must be assessed over a period of at least 4 years and compared with survival and growth of seedlings. The incidence and duration of plagiotropic growth form must be studied in relation to ortet age and other variables.

If tree improvement is envisaged, there will be additional requirements of phenotypic selection and testing of clones. For radiata pine, such a program would take at least 15 years before large quantities of tested clones could be produced (Thulin and Faulds 1968). Meanwhile, maturation of clones will proceed and this could decrease rootability and growth potential (Sweet and Wells 1974) to the extent that those initially selected could no longer be used (Libby 1974a). Techniques for delaying maturation, such as hedging (Libby et al. 1972), must therefore be investigated.

Even a program geared to mass production of reforestation stock would take 10 years to become fully operational, given a 4-year field evaluation and no serious problems with respect to rooting, growth and survival. Moreover, until experience proved it unnecessary, biological risks must be reduced by including many clones in each plantation and, preferably, mixing in seedlings of local origin.

Tissue culture

This review is limited to a discussion of cuttings as a means of propagation. However, in recent years, progress in propagation of conifers by cell and tissue culture indicates that this may eventually be an effective and convenient method for mass propagation of clones (Durzan and Campbell 1974; Brown and Sommer 1975). It is also possible that plantlets which do not arise from pre-existing apical meristems will not possess the maturation related problems inherent with cuttings, i.e., decrease in rooting potential, decrease in growth potential, and plagiotropic growth (Campbell and Durzan 1976). This feature would greatly simplify problems discussed in this review, and there is an urgent need for studies to clarify this important point.

II ACTIVITIES IN VARIOUS COUNTRIES

Japan

Rooted cuttings have been used extensively in Japan since about 1400 and became popular for Cryptomeria japonica (Toda 1974) in many forest regions during the first half of the 17th century. The method of propagation has varied in different areas. In one district, a system of taking cuttings,

with or without roots, from branch layers has been practised for more than 300 years. In another, where climate and soil are favorable for rooting and growth, unrooted cuttings are set directly in plantations and, in a third, cuttings are propagated in nurseries before outplanting. Thujopsis dolabrata cuttings have been planted extensively for a long time and Chamaecyparis obtusa cuttings have been used for many years in one small area (Toda 1974). The magnitude of the program in recent years is impressive. In the 1966/67 planting season, 500 million Cryptomeria plants were used in private forestry in Japan, of which 120 million were rooted cuttings (T. Satoo, pers. comm.). Orchards for the production of cutting material have been established by the Japanese State Government, and by the end of the plus-tree selection program in 1970, the area totalled 800 ha for Cryptomeria. This contrasts to 400 ha of seed orchards produced under the same project (Toda 1974).

Reforestation with cuttings appears to have peaked in Japan and a decline can be expected (Toda 1974). As discussed earlier, it is contended that, compared to clonal stock, the genetically more diversified seedling populations obtained from seed orchards will give an opportunity for leaving a better final crop in plantations where repeated selective thinnings are practised. Also, problems in rooting of cuttings and the greater biological risks using clones are contributing reasons for placing more emphasis on seedling production (Toda 1974).

West Germany

The activity in clonal propagation for practical forestry is centered in Lower Saxony and is directed by Dr. J. Kleinschmit. The emphasis is on genetic improvement of Norway spruce outplanting stock. Initially, 17 000 were selected from 60 million seedlings, but these will be reduced to 1700 through further selection (Kleinschmit et al. 1973). Clones having undergone two selection stages are released for operational planting, and genetic variability is attained by inclusion of many clones (Kleinschmit 1974). Multiclonal varieties have been estimated to give a genetic gain of 40% over the seedling populations normally used (Kleinschmit 1974). An important incentive for using rooted cuttings as the end product of a tree improvement program for Norway spruce is the poor seed production in clonal seed orchards and the long juvenile period preceding cone production.

Techniques for large-scale propagation, using plastic greenhouses, have been developed, and the rooting percentage normally exceeds 90 for 4-year-old ortets (Kleinschmit 1974). In 1972, 240 000 rooted cuttings were raised in Lower Saxony and, in 1973, the total production in West Germany was 1 million plants. It is projected that cutting production in Lower Saxony will constitute 20% of the total plant production of Norway spruce by 1975 and 40% by 1990, out of 5.7 million plants (Kleinschmit 1974).

Finland

Techniques for mass propagation of Norway spruce cuttings have been under study by the Foundation for Forest Tree Breeding since 1962. By using heated plastic greenhouses and intermittent mist, 95% of 150 000 cuttings were rooted in 1972 (Lepistö 1974). Starting in 1969, 1200 clones have been selected from trees 1 to 10 years old and, with further selection, the number was reduced to 300 and finally to the best 60 clones. These will form the basis for mass production. Transplanting of rooted cuttings in the nursery has resulted in a 10-15% mortality, but it is expected that this loss can be reduced by improved techniques. Biological problems in raising rooted cuttings have largely been overcome. However, further evaluation of outplanting problems and an economic appraisal must be made before it can be determined what proportion of the 75 million annual requirement for plants will be satisfied with rooted cuttings (Lepistö 1974).

New Zealand and Australia

More research on biological and technical aspects of using rooted cuttings in forestry has been done in New Zealand and Australia than elsewhere, with the possible exception of Japan, but no practical application has been made. Several researchers have made a case for establishment of radiata pine plantations by this means (Jacobs 1939; Fielding 1963, 1970; Thulin and Faulds 1968; Libby et al. 1972; Shelbourne and Thulin 1974). This pine roots fairly well when young and it is likely that good rootability can be prolonged by special techniques, such as hedging (Libby et al. 1972) and re-propagation (Fielding 1969). However, there remains concern that a genetic gain achieved through use of clonal material is offset by a decrease in growth potential with ageing of the parent trees (ortets), as discussed earlier (Sweet 1973; Sweet and Wells 1974). Further research on rooting and field performance is needed but, with satisfactory results, clonal selection and

mass propagation of cuttings could be effective in plantation improvement of radiata pine (Shelbourne and Thulin 1974).

Canada

Much research has been done on rooting of conifer cuttings, primarily for the purpose of establishment of seed orchards and clone banks. Rauter (1974) has also visualized the use of clonal material of both black and white spruce in reforestation for the Ontario tree improvement program. She submits that the genetic gains should at least offset the higher plant production cost and that rooted cuttings will find a significant place in reforestation in Ontario. One company is considering the use of hemlock cuttings in plantation establishment in British Columbia.

U.S.A.

In California, considerable research is underway on rooting and growth of cuttings of many west coast species and on genetic gains to be obtained by their use in plantations (Libby, pers. comm.). Similar research is also underway with loblolly pine in Texas (van Buijtenen et al. 1975). Ross (1975a, b), working for the Weyerhaeuser Company, devised a method of shearing Douglas-fir seedlings by which an average of 45 rooted cuttings were obtained per 1-year-old seedling. The Company does not presently plan on using this method in reforestation of Douglas-fir, but rather for clonal testing. They intend, however, to use western hemlock cuttings in reforestation (Boyd 1976).

Other Countries

In some parts of Denmark, superior Douglas-fir clones were grafted at a wide spacing in young established plantations to improve their genetic quality during the 1950s and 1960s but this has been discontinued. Interest has now shifted to the use of rooted cuttings. Research on genetic gains and seedling versus clone growth performance for Sitka spruce and Norway spruce is underway (Roulund 1974). Similarly, the potential of a program for establishing plantations with Norway spruce cuttings in southern Sweden is being explored (Samuelson 1975). In France, investigations are progressing on use of cuttings of Douglas-fir seedlings as a supplement to scarce seed supplies of good quality (Franclet 1974). Rooted cuttings of Cunninghamia lanceolata were apparently used extensively in reforestation in South China and Formosa in the early part of the century (Toda 1970). Richardson (1966) noted that some plantations of this species are grown on short rotation south of the Yangtze after establishment by sowing or with closely spaced rooted cuttings.

III THE BRITISH COLUMBIA SITUATION

In B.C., there are active tree improvement programs for Douglas-fir, western hemlock, white and Engelmann spruce, lodgepole pine and Sitka spruce, for which the use of improved clonal stock in reforestation should be considered. Furthermore, reforestation is hampered in some locations by a scarcity of seed of appropriate species or provenance, particularly in high elevation areas on the coast (Reuter 1973), and clonal stock may provide an alternative to seedling stock.

Some pertinent research has been done in B.C. and elsewhere, primarily in the field of cutting propagation, but little information is available on the other important biological considerations discussed previously. Research undertaken and that required for important B.C. reforestation species is outlined below.

Douglas-fir

Agencies involved in studies of cutting propagation include the Pacific Forest Research Centre (PFRC); Canada Dept. Agric., Sidney; MacMillan and Bloedel Ltd.; Pacific Logging Co.; Rayonier Ltd.; Weyerhaeuser Co.; Oregon State University (Horticulture) and University of Calgary (Canadian Forestry Service contract). Some results have been published (Andison et al. 1974; Bhella and Roberts 1974; Black 1972, 1973; Blankensop and Callaham 1960; Brix 1967, 1974; Brix and Barker 1969, 1971, 1973; Cornu 1973; Griffith 1940; Heaman and Owens 1972; Heinrich 1968; Hough 1953; Lanner 1962; Roberts 1969; Roberts et al. 1974; Roberts and Fuchigami 1973; Ross 1975a; Wheat 1964). Much of this work has been done with mature or young trees past the seedling stage, since the problem has been to propagate field-selected plus trees which are usually older trees.

Rooting potential appears to decrease rapidly with age of ortets. Black (1973) found a 100% rooting potential for trees less than 9 years old, and similar good rooting has been found by others (Brix and Barker, unpubl.; Ross 1975a), but the potential

declined to 5% when ortets were between ages 14 and 24 years. Tree-to-tree variation is considerable, with cuttings from some mature trees rooting well (82%) and others not at all (Brix and Barker 1973). Improved techniques have increased rooting of cuttings from mature trees. This is important for seed orchard establishment and breeding purposes, but is of little use for reforestation if maturation drastically reduces the growth potential of cuttings. If this is the case, we must develop techniques that will prolong the juvenile stage of trees, such as hedging, to preserve both the rooting and the growth potential. A continuing repropagation of rooted cuttings may also be effective (Black 1973).

Mass production of cuttings from seedlings is feasible. Sheared seedlings produced an average of 56 cuttings in the first growing season, of which 45 rooted (Ross 1975a). With further propagation of these clones, Ross (1975b) calculated that in excess of ½ million cutting ramets could be produced per seedling clone after only 5 years.

Use of rooted cuttings in reforestation was discussed by Ross (1975b), with special reference to the Weyerhaeuser program. As mentioned in Part I, the merit of using clones rather than seedlings for outplanting in a tree improvement program depends on how important the non-additive genetic component of the total genetic variance is for the trait being selected. Indications are (Ross 1975b) that this is important in Douglas-fir growth and that the genetic gain by using clones from superior genotypes in reforestation could therefore be considerable. Not only would the genetic gain be maximized by using clones but, as pointed out by Ross (1975b), improved stock could become available sooner by vegetative propagation (e.g. perhaps ½ million plants per seedling after 5 years) than from seed orchards that cannot be expected to produce operational quantities of seed for 9 years or more.

In practice, the productive period of selected clones is not likely to begin before the age of 10 years. This is based on starting a 4-year field test with 1-0 seedlings, followed by a 5-year period to build up clones for large-scale production of cuttings. These two procedures could take place concurrently (Ross 1975b), but this would involve considerable extra work in establishing clones for trees which would not be selected on the basis of the field test. After some years of use, perhaps to an age of 15 years, a clone is likely to be replaced by a new improved one. Before a large-scale reforestation program is undertaken, we must know how tree maturation has progressed to this age and affected (a) rootability, (b) growth potential, and (c) growth form. If these properties have been affected, it should be determined whether treatments such as hedging will prolong the juvenile phase. Also to be studied is how early superior stock can be recognized in field tests, i.e., the correlation between juvenile and mature tree growth performance, since we assumed that some selection is possible after only 4 years of field testing.

Present indications are that acceptable rooting can be obtained for trees to the age of 15 years, but there may be a problem in producing plants of suitable form. As discussed earlier, plants from cuttings of mature trees exhibit plagiotropic growth for many years and are unsuitable for reforestation, and even cuttings from young trees may require as long as 6 to 10 years before growth becomes normal (Black 1973). However, shearing of ortets may offer a solution, since this has been shown to improve the form of ramets (Black 1973).

Little is known of maturation effect on growth rate and this is a major deterrent to embarking on large-scale reforestation with rooted cuttings. Copes (1976) found that cuttings from 4- to 8-year-old Douglas-fir grew as well as seedlings during 4 years in the field, but he observed that cuttings from mature plus trees grew considerably slower than those from juvenile trees. As discussed earlier, though growth rate may not be reduced at the age of the ortets when cuttings are taken, the high juvenile growth potential up to that age will be lost unless means to retain juvenility are found.

The following species are discussed less extensively because less information is available, and the same principles and considerations outlined for Douglas-fir also apply to them.

Western Hemlock

Research on rooting is being done by PFRC and by Weyerhaeuser Co. An operational rooting program is being carried out by the latter agency and by the B.C. Forest Service and Rayonier Canada Ltd. as part of their tree improvement programs. Weyerhaeuser Co. intends to use rooted hemlock cuttings in reforestation (20 million plant goal!) because of an insufficient seed supply (Boyd 1976). Few published reports on rooting are available (Brix and Barker 1969, 1975; Wood and Dixon-Nuttal 1954), but good results have been obtained.

By using recommended techniques under well-controlled conditions, an average of about 45% of cuttings from mature trees can be rooted (Brix and Barker 1975) and 90-100% of cuttings from juvenile material (Brix and Barker, unpubl.; Ross, unpubl.), but somewhat less (70%) can be rooted in large-scale operations when only covered nursery beds are used (Boyd 1976). Small cuttings (2-3 cm long) root well and, by shearing the seedlings, mass production of cuttings can be expected to be as prolific for hemlock as for Douglas-fir.

The growth rate of rooted cuttings from mature trees has been slow in the first year or two after rooting, but thereafter good growth has been obtained (Brix and Barker 1975). Juvenile material may do better, especially with improved growing techniques (Ross, pers. comm). No study has been made of maturation effect on growth rates. Some plagiotropic growth has been observed on cuttings from mature trees and, in one trial, one-third of the ramets from various clones still exhibited this form 6 years after rooting (Brix and Barker 1975). However, the problem has been less severe for hemlock than for Douglas-fir cuttings from mature trees. Long-term performance of juvenile cuttings is not known.

Prediction of genetic gain by using hemlock clones in reforestation rather than improved seed sources is not possible at this time, since little information is available on the importance of non-additive genetic inheritance. Some indication of an inheritance of this kind was found for first-year height growth of seedlings, but reliable predictions must await long-term studies in which progenies are grown on a variety of hemlock sites (Meagher 1976). However, any genetic gain obtained in seedling stock can probably be utilized sooner by outplanting rooted cuttings from this stock rather than waiting for production of seed from the seedling seed orchard. The latter is not likely to produce operational amounts of seed until a tree age of 15 years or more unless new techniques for flower promotion are discovered. It is still an open question how early and how well superior hemlock stock can be recognized from field trials. Indications are that the problem of non-genetic variation in clonal stock may be considerable (Ross, pers. comm.).

White Spruce

Most work on rooting of white spruce has been done by researchers in eastern Canada (Day and Breen 1971; Farrar and Grace 1942; Girouard 1971, 1972, 1975; Rauter 1971). Rootability is good for seedling material but decreases rapidly with older material. Thus, 77% of cuttings from 3-year-old seedlings rooted (Rauter 1971) and 52 and 18% rooted from 7- and 19-year-old trees, respectively (Girouard 1971).

A program for using rooted cuttings in tree improvement and reforestation in Ontario was outlined by Rauter (1974). This is based on selection of 3-year-old seedlings in operational nurseries with an intensity of 1:100 000 for seed sources from 6 site regions. The selected seedlings plus controls are transplanted into holding areas and cuttings from them are rooted within 2 years. The rooted stock is grown for 2-3 years before being outplanted for field testing in 2 locations for each of the 6 site regions. The best clones in this test will be repropagated by cuttings for use in reforestation. A continuing selection of seedlings will be made in the nurseries, thus adding new clones while old ones are eliminated. According to this schedule, 8 years are required for establishment of a field test. Add to this a testing period of 4 years, and a physiological age of 12 years is reached before the clones can be used in reforestation. By then, decreased rooting potential, and possibly decreased growth rate, will be encountered. Further research is required to clarify and overcome these problems, or to demonstrate the feasibility of reducing the selection period.

Lodgepole pine

Rooting studies with this species are being conducted by the British Forestry Commission and by the University of Calgary (CFS contract). Some success with rooting of needle fascicles from seedlings has been reported (Larsen and Dingle 1969). With the best treatment, 20% of fascicles rooted, but only 5% survived and produced terminal growth. Stem cuttings have yielded better results, with a maximum of 80% rooted for mixed clones (Longman et al. 1972). The ages of the clones were not stated. There is no published information on growth form, but rooted cuttings of pine species usually do not exhibit plagiotropic growth.

Lodgepole pine, an early and prolific seed producer, develops cones in open-grown stands 5-10 years old and good cone crops can be expected at 1- to 3-year intervals (Fowells 1965). There would not, therefore, be any reason for using cuttings because of a scarce seed supply, and genetic gains

obtained through tree breeding can be utilized quickly by establishing seedling or clonal seed orchards. Whether non-additive genetic inheritance is important enough to warrant use of cuttings is not known.

Sitka spruce

A rooting potential of 100% was found by Griffith (1940) for cuttings from young, vigorous Sitka spruce trees; moreover, root formation can sometimes occur in less than 3½ weeks (Longman et al. 1972). Plagiotropic growth does not appear to be a problem with cuttings from young trees, and ramets of the same clones were uniform in early growth performance (Roulund 1974). This uniformity is favorable for selection of plus stock in clonal tests, as well as for use of clones in reforestation. Effects of maturation on growth rate are not known.

Seed production begins in 20- to 40-year-old stands with a few cones in the upper crown (Fowells 1965). Following this slow start, Sitka spruce becomes a prolific seed producer, yielding a good crop every 3 to 4 years and light crops in between. This late cone production is an incentive to use cuttings from plus seedlings in reforestation.

Sitka spruce appears to be a good candidate with regard to cutting use in reforestation, because of ease of rooting, lack of plagiotropic growth, apparent uniform growth performance of clones, and late seed production.

Yellow Cedar

Problems in obtaining planting stock of this desirable high elevation species, because of low availability and poor seed germination, have prompted studies of cutting propagation by B.C. Forest Service and PFRC. Karlsson (1974) obtained an average rooting percentage of 89 for cuttings from 3- to 10-year-old trees from several provenances and similar good rooting results have been achieved at PFRC (Edwards, pers. comm.). Plantable stock was produced in one growing season. Other aspects pertaining to cutting use in reforestation have not been studied.

IV CONCLUSIONS AND RECOMMENDATIONS

Rooted cuttings can be used in reforestation for two purposes, (1) to supplement scarce seed supplies, and (2) as a means of tree improvement.

Seed shortage may justify the use of cuttings on a short-term basis. However, the cost of producing rooted cuttings is likely to remain considerably higher than it is for seedlings. The lowest estimate at present is a 30% higher cost on a mass-production scale for Norway spruce cuttings. Also, risk of failure is higher with cutting than with seed propagation. An economic analysis is needed but, on a long-term basis, we may be better off by planning for adequate seed supplies (i.e., by establishment of seed orchards, supporting research on stimulation of cone production and improvement of cone collection techniques) and by supporting research on seed germination for species where this presents a problem (i.e., hemlock, yellow cedar, true firs).

With regard to tree improvement, cuttings have the advantage that they retain non-additive genetic qualities, whereas only additive variance is retained by seedlings. Furthermore, genetically improved stock can be mass propagated and utilized quickly by cutting (e.g., a calculated ½ million plants originating from one Douglas-fir seedling after 5 years), but it may take 15 years or more for some species, such as Sitka spruce, before commercial quantities of seed can be produced in a seed orchard. This advantage of using cuttings is likely to diminish with more research on stimulation of early cone production; remarkable progress has been achieved in recent years with some species.

On a long-term basis, therefore, the incentive for using cuttings depends primarily on the importance of non-additive genetic inheritance. Reliable estimates of this are not available for British Columbia tree species, although indications are that it is of some importance in early growth of Douglas-fir and western hemlock. High priority must be assigned to studies of heritability, which will also be needed for evaluating other aspects of tree improvement programs. Apart from genotypic improvement, advantage can be taken of improvements associated with maturation of parent trees; e.g., some wood qualities and resistance to some insects and diseases. At present, there is no indication that this will be an important consideration for B.C. trees. Lastly, clones produced by cuttings can provide a genetically more uniform population which, in addition to having growth superiority, may have advantage in wood utilization.

Some disadvantages of rooted cuttings which, depending on species, may weigh against these

possible benefits are: (1) higher cost, (2) poor or inconsistent rooting potential for many species with all but very young parents, (3) inherent poor growth form (plagiotropic growth) for many years, especially with parent material beyond the juvenile stage, (4) a possible decrease in growth potential with increase in parent age, and (5) a limited genetic variability which, apart from giving certain advantages as mentioned above, may result in biological risks in regard to site adaptation and resistance to insects and diseases.

As indicated previously, some of the disadvantages are not present for all important B.C. species and the seriousness of others has not been properly assessed. Some problems can probably be avoided (e.g., item 5) or limited or overcome by further research.

Following is a list of research studies required before long-term benefits and problems of using cuttings in reforestation can be fully evaluated:

(1) mode of inheritance of growth characteristics

(2) feasibility of selecting genetically superior stock at an early age

(3) rooting potential in relation to maturation

(4) growth rate in relation to maturation

(5) growth form in relation to maturation

(6) techniques for prolonging the juvenile growth phase or reversing the mature to the juvenile phase.

In addition, alternative ways of deriving the benefits, or avoiding the problems, of cutting use should be investigated; these are:

(1) vegetative propagation by means of cell and tissue culture and its effect on avoidance of maturation

(2) promotion of early and abundant cone production in seedling and clonal seed orchards.

Although all of these studies are major undertakings requiring considerable time and resource input, they are of fundamental importance in solving important forestry problems, other than the one under review.

Opportunities for successfully using rooted cuttings in reforestation are present, but lack of knowledge dictates caution. Much research is needed before more than small pilot-scale outplanting trials should be considered.

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